habitat this should be, in its cleistogamous-flowering summer state, the *V. clandestina* of Pursh.

GROUP III. Subcaulescent by leafy stolons, or caulescent, with ascending 2-3-leaved stems, slender, almost glabrous, multiplying by long filiform root-stocks: leaves all reniform or cordate, undivided: corolla a bright yellow, with saccate spur: stigma terminal, beardless and beakless.

V. sarmentosa Dougl. To this belongs *V. rotundifolia* Hook. in Lond. Jour. Bot. vi. 73, in Geyer's collection, a species which it considerably resembles at first, flowering direct from the root-stock.

V. biflora L. Always caulescent, no leafy stolons; stigma margined on two sides. In this country known only from the Colorado Rocky Mountains; in the Old World ranges from Kamtschatka and Japan to Europe.

Synopsis of North American Pines, based upon leaf-anatomy.[1] I.

JOHN M. COULTER AND J. N. ROSE.

(WITH PLATE VIII.[2])

The genus Pinus is very naturally circumscribed, but its species have always been notably difficult of discrimination. This has arisen partly from the real difficulty of the subject, partly from the imperfect material found in our collections, and mostly from the insufficiency of the characters used. The oldest division of the genus was based upon the number of leaves in the bundles, and this must still be considered a supplementary character of considerable importance. In late years, however, it has been discovered that most valuable characters are to be found in the internal structure of the leaves, meaning, of course, the secondary or foliage leaves. The great diversity in the structure of these leaves is in marked contrast with the uniformity found in leaves of higher plants, and of itself is no mean argument in defense of the position of gymnosperms as the lowest of phanerogams.

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[1]Read before the A. A. A. S., Buffalo meeting, 1886.

[2]EXPLANATION OF FIGURES.—1. *P. Strobus*, 2 dorsal peripheral ducts, stomata on ventral faces, and single fibro-vascular bundle, X54; 2. *P. clausa*, 2 parenchymatous ducts, stomata on all faces, and 2 fibro-vascular bundles, X54; 3. *P. Cubensis*, internal duct, X54; 4. *P. Arizonica*, 3 cells of the bundle-sheath with thick outer walls, X250; 5. *P. monophylla*, thin-walled bundle-sheath, X250; 6. *P. aristata*, strengthening cells next the epidermis, X250; 7. *P. flexilis*, thin-walled layer (pitted) next the epidermis, X250; 8. *P. tuberculata*, thin-walled layer between epidermis and strengthening cells, X250.

In 1865 F. Thomas, in Pringsheim's *Jahrbucher*, iv. pp. 23-63, first called attention to these leaf characters as means of classification. The other authors upon this subject have been C. E. Bertrand, *Bull. Soc. Bot. France*, xviii. pp. 376–381, 1871, and *Ann. Sci. Nat. Bot.*, xx. pp. 5–153, 1874; W. R. McNab, *Proc. Irish Acad.*, ii. pp. 209–213, 1875, and in the same journal, pp. 673–704, 1877; E. Purkinje, of Austria, has also made studies, but his results have not been learned. Probably the most diligent and successful investigator of this subject was the late Dr. Geo. Engelmann, whose name in connection with this group of plants is the most familiar in this country. Some of his conclusions have been published in his "Synopsis of American Firs," published in 1878 in the *Trans. St. Louis Acad.*, iii. pp. 593–602, and particularly in his "Revision of the genus Pinus," published in 1880 in the same journal, iv. pp. 161–189. It is upon this last contribution that the work recorded in the present paper was based. Dr. Engelmann made use of the characters obtained from leaf-structure to define many of his subdivisions of the genus, but did not carry them on into the species. Our object has been, in the first place, to verify his work; in the second, to make use of these characters in the discrimination of species.

No reference will be made to any other than leaf characters, but it is far from the intention to claim that other characters are to be discarded. The leaf characters are rather given as confirmatory and supplemental, and in some doubtful cases decisive. The permanency of these internal structural characters, as compared with those which are external, is evident, but even with this, care should be taken not to place too implicit confidence in them. They should be used in connection with the ordinary external characters, though it is claimed here that almost all species of pines can be determined by a single leaf. The value of such characters is thus seen, not only in confirming those obtained from scales and cones, but in deciding upon our too numerous herbarium specimens which lack complete material, or in fossil botany in the determination of species or relationships. In several cases it will also be noted these characters serve to separate forms which have been doubtfully placed together, and more frequently to bring together certain forms which have been kept apart as doubtful species.

It will be observed that Dr. Engelmann's arrangement, in the main, has been confirmed, trifling modifications here and there being made to better express what is conceived to be true relationships. The necessity of a lineal arrangement, of course, distorts many of the facts, but we believe it to be the most natural yet suggested.

The number of species of American pines, exclusive of Mexico, as given by Prof. C. S. Sargent, in the tenth census report, is thirty-five. These have all been examined, as well as eight or ten Mexican species, which are also included. The material has been obtained from the Harvard herbarium, from other well known herbaria, and also from the very instructive slides prepared by the Rev. J. D. King, whose material was obtained from Prof. Sargent. Effort was made to obtain material from as wide a range as possible, and repeated studies of the same forms were constantly made.

Transverse sections of the leaf are used, and these should always be made well away from either its base or apex. Neglect of this precaution has led to confusion, as a leaf with two distinct fibro-vascular bundles, may be thought to have but one if the section is made near the extremities. The bundles usually separate above the base of the leaf, and blend again near its apex, and in poorly developed leaves may never appear separate at all. This led Dr. Engelmann to say that the single or double bundle "is of very little diagnostic importance, as we find occasionally single or double bundles in the same species,"[1] while, with the precaution mentioned, we have known it to fail but once.

The outline of a transverse section, in the main, depends upon the number of leaves in a fascicle, but this can not be pressed too far. In P. monophylla the outline is nearly circular, in 2-leaved species it is semicircular, in 3-leaved species triangular, but in 5-leaved species it is also triangular. It is thus usually possible to determine approximately the number of leaves in a fasicle by the transverse section of a single one, and hence the number of leaves will also be legitimately included among our anatomical characters.

The leaf-structure is separable into three regions, the cortical, the mesophyll and the fibro-vascular.

I. *The cortical region.* This is composed of one layer of epidermal cells, with very thick walls, interrupted here and there by stomata. The position and number of rows of stomata are valuable characters. In some species, as P. Strobus, they are found only on the ventral side; in others, as in P. Coulteri, they occur both dorsally and ventrally. The rest of the cortical region is made up of the so-called "hypoderma," being mostly very thick-walled cells, aptly called by Engelmann "strengthening cells" Engelmann rejected the term "hypoderma," because cells of the same nature often occur about the resin ducts and in the fibro-vascular region. The term "strengthening cells," therefore refers to this thick-walled tissue wherever found, and they may be cortical, about the

[1]Trans. St. Louis Acad., iv. 165.

ducts, or central. The term "hypoderma" still has its use, however, as it contains another group of cells which we have called "thin-walled cells," to distinguish them from the strengthening cells. This thin-walled layer frequently occurs between the epidermis and the cortical strengthening cells, and its presence or absence is a character of considerable importance. Seven of our species have an hypoderma composed only of these thin-walled cells, with no cortical strengthening cells; eight or nine species have no thin-walled layer between the epidermis and the cortical strengthening cells; while the remainder have the thin-walled layer between the epidermis and strengthening cells. By "thin-walled cells" it must be understood that we are speaking comparatively, as they are by no means thin-walled in fact, but contrasted with the epidermal and strengthening cells are decidedly so. Rarely is there any difficulty in distinguishing this layer, but occasionally, as in P. monticola, the thin-walled layer shades into the strengthening cells.

II. *The mesophyll region.* This is chiefly composed of large chlorophyll-bearing parenchyma cells, with very characteristic infoldings, which are of no diagnostic value. In this region, however, are found the resin ducts, and their position and size furnish very important characters They are found in three positions, viz.: *peripheral*, when they lie next to the cortical region; *parenchymatous*, when completely surrounded by the mesophyll; *internal*, when next to the bundle-sheath. The terms "external," "medial," and "internal" would better express their relation to the mesophyll region, but the former terms were given by Dr. Engelmann, and there is no good reason for changing them. A little confusion in these terms also arises from the fact that in two species resin ducts have been occasionally discovered in the fibro-vascular region, viz.: P. sylvestris,[2] to which we add P. serotina. Dr. Engelmann considers the positions of these ducts in the mesophyll region as the most useful diagnostic character obtained from the leaf-structure. However, even this character can not be relied upon exclusively, as variations from the normal position are apt to occur. This variation does not consist in changing the normal position, but in the development of accessory ducts in some other position, or in the change in position of a single one of the normal ducts. To Dr. Engelmann's list of these variations we have added ten or twelve species, showing that such variation is not unlikely in the whole genus. All the resin-ducts are lined with a layer of thin-walled secreting cells, outside of

[2]Arthur, Barnes and Coulter, Hand-book of plant dissection, p. 167.

which, in many cases, are thick-walled strengthening cells, either scattered about the duct or forming a compact sheath.

III. *The fibro-vascular region.* A very distinct bundle-sheath invests this region, the cells of which are either comparatively thin-walled, or with the outer wall excessively thickened. This has been a useful character in some of our subdivisions, but is not always constant. P. Sabiniana, P. Coulteri, and a few others may or may not have the bundle-sheath with thickened outer walls. In the center of this region occur the fibro-vascular bundles, either one or two. This character we have used as one of the best for separating the genus into two sections. As has been mentioned, Dr. Engelmann considered it of but slight diagnostic importance, but we have found no character less likely to fail. In the examination of many hundreds of sections but one was different from the expectation in this regard. The bundles are always together at the base and apex of the leaf, and may be widely separated during the remainder of their course, but even when they are in contact they can easily be distinguished as two. In the use of the terms "dorsal" and "ventral", when speaking of the leaf surfaces, the former is applied to the phloem side, the latter to the xylem. Strengthening cells may or may not be found about the fibro-vascular bundles, and this is such a constant character as to be of good service in classificatiou. The rest of the fibro-vascular region is filled with parenchyma cells and tracheids, neither of which are of any diagnostic value.

Using the structural characters described the following synoptical arrangement of our pines, including some Mexican species, is presented, for the purpose of supplementing other characters, for use in the absence of other characters, and to indicate relationships.

§1. Fibro-vascular bundle one: leaves mostly in fives.

*A thin-walled layer next the epidermis (somewhat thickened in P. monticola): no strengthening cells next the epidermis nor about the ducts: leaves always in fives.

† Stomata on dorsal side of leaf.[3]

1. **P. albicaulis** Engelm. Epidermis mostly very thick-walled: one to three rows of dorsal stomata: two dorsal ducts (.050–.070 mm.); often a ventral duct, sometimes one or more smaller accessory ones: thin-walled cells about ducts larger than those next the epidermis: leaves 2 in. long.

Along the Coast Range, from California to British Columbia.

[3] This does not mean that there are no ventral stomata.

First described by Engelmann in *Trans. St. Louis Acad.*, ii. 209; then reduced by him to a variety of the next species in *Bot. Calif.*, ii. 225; finally restored to specific rank by the same author in BOT. GAZETTE, vii. 4. Several specimens labeled P. aristata in herbaria belong here.

2. **P. flexilis** James. Epidermis not so thick-walled: one to four rows of dorsal stomata: two dorsal ducts (.030–.045 mm.); rarely a ventral one: thin-walled cells about ducts equalling those next the epidermis: leaves 2–4 in. long.

Western slope of Rocky Mountains to California.

The extreme forms of these two species stand well apart, but there are intermediate forms which are hard to determine.

† † No stomata on dorsal side of leaf (often present in P. monticola).

3. **P. reflexa** Engelm. Three or four rows of stomata on ventral faces: two dorsal ducts (.025–.040 mm.): number of cells in bundle-sheath 16–20: fibro-vascular bundle often quite large, almost filling the fibro-vascular region, which often has strengthening cells, differing in this respect from the other species of the group and resembling P. cembroides: leaves 1–2 in. long.

High mountains of New Mexico and Arizona.

First described as a variety of P. flexilis by Engelmann in *Bot. Wheeler's Report;* then raised to specific rank in BOT. GAZETTE, vii. 4.

4. **P. Strobus** L. Three to five rows of stomata on ventral faces: one to three ducts (.035–.040 mm.), mostly two and situated half way between the middle and edge of the dorsal face; when three the odd one is on one of the ventral faces: number of cells in bundle-sheath 15–19, mostly 16: leaves 3–4 in. long.

Along the Alleghanies and in the northern states east of the Mississippi.

5. **P. Ayacahuite** Ehrenberg. Much like the last, but with a few more cells in the bundle-sheath (18–21), and always two dorsal ducts, which are much smaller (.015–.025 mm.).

Mountains of Mexico.

6. **P. monticola** Doug. Two to six rows of ventral stomata, often one or two dorsal rows: mostly two dorsal ducts (.025–.050 mm.), sometimes but one; often a few ventral ducts: number of cells in bundle-sheath 20–25: leaves 2–4 in. long.

Mountains of the Pacific slope.

The thin-walled layer next the epidermis, which is characteristic of this group, is not so evident as in the other species, but can be distinguished from the strengthening cells. It marks well a transition phase to the next group.

* * No thin-walled layer next the epidermis: strengthening cells next the epidermis and generally about the ducts: leaves one to five.

† Stomata on dorsal side of leaf.

7. **P. Lambertiana** Doug. Two to six rows of stomata on each face of the triangular section: always two dorsal ducts, often one between, occasionally some ventral ducts which are sometimes parenchymatous, no strengthening cells in fibro-vascular region: leaves 3–4 in. long.

In the Sierra Nevada and Coast Range.

Notes on the mode of pollination of Asclepias.

CHARLES ROBERTSON.

(WITH PLATE VIII)

In regard to the visitors of Asclepias Cornuti, Dr. Hermann Müller observes that they "slip upon the smooth parts of the flower until a foot enters the wide inferior part of the slit, in which it at last gets a firm hold".[1] Mr. T. H. Corry[2] describes the insect as grasping the back of a nectary, and plunging its proboscis into its cavity, "endeavoring at the same time to get a firm and sure foothold on the unstable flowers", until the insect at length places one of its feet into the wider part of an alar fissure.

Having collected insects on the flowers of six species of Asclepias, I regard the normal action of the most common and most efficient to be that they hold on to a flower, or several flowers, in such a way that their feet go down below the angles of the alæ, and when the legs are drawn upwards they are caught between the strongly projecting hoods and guided by them over the entrance of the stigmatic chamber, which occupies the narrow interval between their bases. Of native insects, the most common visitors I have observed on A. Sullivantii, are humble bees (Bombus separatus, B. Pennsylvanicus, and B. scutellaris) and Danais Archippus. The feet of humble bees reach down as far as the bases of the petals, and I have often found the pollinia fastened upon their tibial spurs as well as on their claws. I have also found pollinia of this species on the spurs and claws of Danais Archippus, and high up on tarsal hairs of Prionony x

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[1] "Befruchtung der Blumen", 1873, p. 336. "The Fertilization of Flowers", translated by D'Arcy W. Thompson, B. A., 1883, p. 398.

[2] "Structure and Development of the Gynostegium and on the Mode of Fertilization in Asclepias Cornuti, Dec.," Trans. Linn. Soc. Lond. Bot. 2d Ser. Vol. II., part 8. 1883, pp. 186, 187.